

The Bandwagon Effect: Conspecific Attraction and Vulnerability to Ecological Traps

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ABSTRACT

Many animals assess habitat quality using indirect cues. These cues may be reliable indicators ordinarily, but when humans alter the environment, animals may prefer unsuitable habitats. Such ecological traps may be especially problematic for animals that settle preferentially near conspecifics. This mechanism of habitat selection, called conspecific attraction (CA), could lead to heightened extinction risk if individuals caught in the trap lure too many additional settlers. Any such “bandwagon effect” could be ephemeral, though, because individuals that do settle in better habitats should be more successful and so these habitats might accumulate more individuals over the long run. The population could then escape despite an initial congregation of entrapped individuals. We ask whether CA, compared with other mechanisms, may provide such an escape. Only philopatry, preference for the natal habitat, provides a consistent escape. CA performs poorly because individuals lure one another reiteratively into traps. In the face of global change, it is important to recognize how ordinarily adaptive mechanisms of choice can compromise population growth under novel conditions. Such Allee effects may be especially pronounced when individuals seek the company of conspecifics. We highlight the need to avoid setting ecological traps, particularly for species prone to the bandwagon effect.

Keywords: Allee effect; extinction; habitat selection; ideal despotic distribution; philopatry; Weber’s Law

INTRODUCTION

Animals often use indirect cues as indicators of habitat quality. This reliance on indirect cues makes them vulnerable to fitness losses when habitat modification uncouples these cues from the suitability they traditionally represent. An ecological trap (Schlaepfer *et al.*, 2002) is set when an individual preferentially selects now-poor habitat over available high-quality habitat in response to indicators of quality that were reliable throughout the organism's evolutionary history. Traps may arise via amplification of the cues, reduction in habitat quality, or both (Robertson & Hutto, 2006). Anthropogenic modifications to the environment readily produce all of these effects, making ecological traps of paramount concern to conservationists.

Examples of such ecological traps are numerous. Attracted to the reflection of horizontally polarized light, mayflies sometimes lay their eggs on asphalt rather than water and so suffer complete reproductive failure (Kriska *et al.*, 1998). Attracted to nest sites in residential areas, snapping turtles suffer from sex-ratio distortion (Kolbe & Janzen, 2002). Attracted to warm water near power plants, manatees get stranded in cold water during sporadic plant shutdowns (Shane, 1984). Attracted to edge habitat along clearings (e.g. Weldon & Haddad, 2005), many breeding birds suffer increased risk of nest predation and brood parasitism, sometimes resulting in complete reproductive failure. These examples barely begin to convey the vast potential for setting new ecological traps in our changing world.

Trapped populations may dwindle, to the point where social dysfunction exacerbates the situation. Such behaviour-mediated Allee effects (Allee, 1931; Courchamp, 1999; Stephens & Sutherland, 1999), where individual fitness declines with shrinking population size/density, seem to be prevalent. If a population falls below a threshold size/density, various vital functions may be disrupted (e.g. social thermoregulation, antipredator vigilance, mate-finding, and inbreeding

avoidance). Individuals lose these social benefits and reductions in individual fitness often translate into reduced population growth.

Kokko & Sutherland (2001) modeled an ecological trap by degrading the quality of an initially preferred habitat. They explored the potential of several habitat-selection rules to provide an escape. When individuals continued to assess habitat quality according to old knowledge, they distributed themselves in ways that inhibited population growth (Battin, 2004). This Allee effect often led to extinction, but Kokko & Sutherland did find that some simple behavioural mechanisms could provide an escape. Most notably, simply preferring the natal habitat (philopatry) provided the most effective escape, performing virtually as well as habitat selection based on perfect knowledge of the new conditions.

Here we extend this work to ask whether another mechanism – conspecific attraction (CA) – may also provide an effective escape from ecological traps. The presence of conspecifics may typically signify a habitat where individuals with similar ecological demands have succeeded and so conspecific cues may serve as an adaptive heuristic (Smith & Peacock, 1990; Danchin & Wagner, 1997). Most empirical work on CA has focused on birds (e.g. Muller *et al.*, 1997; Sergio & Penteriani, 2005; Ahlering *et al.*, 2006; Borque & Desrochers, 2006), and ornithologists have celebrated CA's value as a conservation tool because attracting individuals using conspecific cues (e.g. models, calls) may be more effective than increasing the availability of suitable habitat (Ahlering & Faaborg, 2006). However, settling near conspecifics could backfire if the residents – or conservationists – have misassessed habitat suitability. Individuals settling near conspecifics in poor habitat will increase the attractiveness for subsequent settlers. We call this the bandwagon effect, borrowing the term from the social sciences where it connotes that people's preferences for commodities tend to strengthen as more people purchase them. We

ask whether CA may help populations escape ecological traps or if the bandwagon effect tends to drive them toward extinction.

SIMULATION METHODS

Background

Following Kokko & Sutherland (2001), we simulate the response of a population occupying two habitat patches, an initially high-quality habitat A and a low-quality habitat B. Habitat A undergoes deterioration at the beginning of the simulation, whereas the quality of habitat B remains fixed throughout.

Imagine that prior to any change in habitat quality individuals arrive and settle onto territories according to the ideal despotic distribution. That is, the first individual to arrive settles in the best vacant territory, in habitat A. The next individual settles in the next-best vacancy in habitat A, unless the best vacancy in habitat B is a better choice. Likewise, the next individual to arrive chooses the best vacancy available, whether in habitat A or B. In this way, each individual chooses the best option for itself and the ideal despotic distribution emerges.

Now consider what might happen if the higher-quality habitat A undergoes a reduction in quality. If early-arriving individuals choose habitats based on old information (i.e. without knowledge of the degradation of habitat A), then a behavioural Allee effect could arise. That is, individuals will settle in less-than-ideal vacancies and population growth will be suppressed. The population could fail to escape the ecological trap. Conversely, if the settlers were to use new information, then the ideal despotic distribution will be achieved and the population will simply avoid the ecological trap. We consider these scenarios, old (obsolete) versus new (perfect) information, as endpoints of a continuum. We then consider three simple habitat-

selection mechanisms (philopatry, learning, and conspecific attraction) that might allow for escape from the ecological trap.

Simulation details

Individuals settling in better territories experience higher productivity (i.e. higher probability of producing fledglings). We assume the productivity f of the n^{th} occupied territory in habitat A is given by

$$f_A(n) = 0.75 \left[1 - (0.00167n)^{1.8} \right], \quad (1)$$

which generates a density-dependent decline in productivity. That is, average breeding success declines as territories of lower quality must be occupied by later-arriving breeders.

The productivity in habitat B is 15% lower than that in habitat A prior to the reduction in quality of A (i.e., productivity of the n^{th} territory occupied in B equals 0.85 multiplied by the right-hand side of eq. [1]). Individual i prefers habitat A according to its perception of the relative quality (productivity) of the habitats,

$$P_i = f_A(n) / f_B(n), \quad (2)$$

which is independent of n . Thus, if $P_i > 1$, the individual will prefer habitat A, and if $P_i < 1$, it will prefer habitat B. P_i is an estimate of the individual's overall assessment of the quality of habitat A versus B, but we assume each individual also takes into account the relative quality of the next best territory available (vacant) in the two habitats. We assume that the decision to settle in habitat A versus B depends on the preference P_i multiplied by relative territory quality. That is, individual i will occupy the next best vacancy in habitat A if

$$P_i f(n_A) > f(n_B), \quad (3)$$

and the next best vacancy in habitat B if the inequality is reversed.

At the beginning of the simulation, the productivity of all territories in habitat A is degraded by proportion α (here, either 35 or 40%). Now, old preferences (eq. [2]) would lead to a non-ideal choice of habitat A and place the population in the ecological trap. At the other extreme, we consider the possibility that individuals can perfectly assess the new conditions. In this case, the optimal preference following degradation of habitat A is given by

$$P_i = (1 - \alpha) f_A(n) / f_B(n), \quad (4)$$

which leads to the ideal despotic distribution. Again, we consider these two habitat-selection rules, old and new preferences, as endpoints of the possibilities.

Kokko & Sutherland (2001) simulated the response of the population to reduction in the quality of habitat A based on these two rules:

- 1) Old (formerly optimal) preferences: unchanged preferences, with P_i s based on equation (2) (i.e. individuals have no knowledge of the reduction of the quality of habitat A).
- 2) New (currently optimal) preferences: new preferences, with P_i s based on equation (4) (i.e. individuals have perfect knowledge of the reduction in quality of habitat A).

They also considered alternative rules:

- 3) Learned preferences (phenotypic plasticity): offspring have no knowledge of the reduction in quality of habitat A and so their initial preferences are given by equation (2); however, an individual that breeds successfully will prefer the current habitat in the next attempt (i.e. $P_i = P_c$ if breeding in habitat A, and $P_i = 1/P_c$ if breeding in habitat B, where the

subscript c connotes current). An individual that fails will prefer the alternative habitat in the next attempt. We assume $P_c = 1.2$.

- 4) Philopatric preferences: individuals maintain a constant preference for the habitat in which they were born (i.e. if born in habitat A, then the individual will prefer that habitat with magnitude $P_i = P_b$ [> 1], and if born in habitat B, the individual will prefer habitat B with the same magnitude, $P_i = 1/P_b$, where the subscript b connotes born). We assume $P_b = 1.2$.

We replicate the original simulations, based on these four habitat-selection rules (and ignoring a fifth rule, genetically inherited preferences, which we omit for simplicity.) We add one new rule to evaluate the potential for conspecific attraction to provide an escape.

Conspecific attraction

We initially consider three rules for choosing habitat based on conspecific cues. All three rules assume individuals are naïve about the reduction in quality of habitat A. They all assume early-arriving individuals make habitat choices based on old preferences (eq. [2]), and later-arriving individuals take into account the number of individuals currently occupying habitat A (N_A) versus B (N_B) when choosing where to settle. For a comparison of the hypothetical probabilities of choosing either habitat A or B at varying combinations of population sizes, see Fig. 1.

Weber's Law. When at least one individual has arrived in each habitat, the quantity of individuals in each habitat creates a sensory impetus that drives preferential choice. Weber's Law describes the cognitive assessment of differences in magnitude, which are more readily discernable for small quantities. In this context, differences between numbers of conspecifics in habitats A versus B should be more readily discernible at lower densities. For example, the

difference between 5 and 10 conspecifics is more detectable than the difference between 105 and 110. We assume the ability to detect a difference and hence choice is described by a logarithmic function (Shettleworth, 1999):

$$\Pr(A) = 0.5 \log(N_A / N_B) + 0.5. \quad (5)$$

We assume if $N_A/N_B > 10$, then the individual chooses habitat A; if $N_A/N_B < 1/10$, then the individual chooses B. If $N_A = N_B$, habitats A and B are equally likely to be chosen; otherwise, preference favours the more heavily occupied habitat.

To implement this rule, we must specify the choices made by early-arriving individuals. The first individual to arrive chooses a habitat based on its valuation of the next best territory available in habitat A versus the next best territory available in habitat B, according to:

$$\Pr(A) = 1 - (1 + \exp[f_A(n+1)P_i - f_B(n+1)])^{-1}. \quad (6)$$

The next individual(s) to arrive also uses this rule, until both habitats contain at least one settler. From that point on, Weber's Law dictates choice. Thus, the initial rule (eq. [6]), based on old information, ignores conspecific cues, until a comparison between N_A and N_B becomes possible (i.e. when both habitats become occupied by at least one settler). Then we assume all subsequent choice is dictated by conspecific cues (eq. [5]) and hence not by habitat quality per se.

Stamps. Habitat choice for the first individuals follows equation (6), as described above. To model the effect of conspecific cues on habitat choice, Stamps *et al.* (2005) used an expression similar to equation (6), but it included a term $\beta = N_A - N_B$ to incorporate the effect of CA:

$$\Pr(A) = 1 - (1 + \exp[f_A(n+1)P_i - f_B(n+1) + \beta])^{-1}. \quad (7)$$

A larger positive value for β translates into a stronger attraction to conspecifics in habitat A.

Weber-Stamps. The first individuals' decisions remain the same as for Weber's Law above, and later-arriving individuals follow a modified version of the Stamps rule. In this version, the conspecific-attraction term is now log-transformed (i.e. β is replaced by $\log[N_A] - \log[N_B]$):

$$\Pr(A) = 1 - \left(1 + \exp\{f_A(n+1)P_i - f_B(n+1) + [\log(N_A) - \log(N_B)]\}\right)^{-1}. \quad (8)$$

This modification incorporates the non-linearity described by Weber's law and dampens conspecific attraction at large N . For example, the relative attractiveness of habitats with 100 versus 10 individuals is identical to that of habitats with 1000 versus 100 individuals (i.e. in both cases, the quantity within square brackets equals unity).

Life histories and catastrophes

We consider two life histories, one fast (annual adult survival $S = 0.5$, brood size $B = 4$) and the other slow ($S = 0.8$, $B = 1$). Juvenile survival is half that for adults. Both strategies would lead to the same lifetime reproductive success in a common habitat.

We also consider the effect of stochastically occurring catastrophes. We model the potential for escape from ecological traps in the presence of such catastrophes, which we assume reduce both adult and offspring survival by 50%, and occur with probability $C = 0.03$ in each year.

DATA ANALYSIS

We used Kolmogorov-Smirnov (K-S) tests to compare cumulative frequency distributions of final population size, and Fisher's exact tests to compare proportions of populations that went extinct. These tests used SPSS (2006) routines and were two-sided. To compensate for the multiplicity of tests performed, we evaluated the significance of our results using the Benjamini & Hochberg (1995) method. Any nominally significant (i.e., $P < 0.05$) test is considered to remain significant provided $p_i \leq iq/m$, where $p_1 \leq p_2 \leq \dots \leq p_m$ are the ordered P -values, q is the assigned false discovery rate (0.05), and m is the number of tests conducted. Virtually all of the results reported as significant remained so after this adjustment. We point out two exceptions.

RESULTS AND INTERPRETATION

Conspecific-attraction rules

The conspecific-attraction (CA) rules behaved similarly. Across all combinations of habitat-quality reduction and life-history speed and with catastrophes present, median final population size fell within a narrow range (i.e. 109-137). Pairwise comparisons of distributions of final population size were nonsignificant (K-S test: $P_s > 0.35$), except for Weber-Stamps compared with Weber ($P = 0.009$) and with Stamps ($P = 1.4 \times 10^{-24}$), for 35% quality reduction and fast life history. For these conditions, Weber-Stamps outperformed the other rules in terms of final population size, but not in terms of extinction rate (Fisher's exact test: $P_s > 0.36$; rates: 4%, Weber-Stamps, 3%, Stamps, and 1%, Weber). Across all conditions, extinction rates were statistically indistinguishable among rules ($P_s > 0.09$).

We arbitrarily use the Weber-Stamps rule (eq. [8]) to evaluate the potential for CA to provide an escape from the ecological trap. This rule performed better for the faster life history in terms of final population size (40% reduction: $P = 0.005$; 35%: $P = 2.1 \times 10^{-8}$), but not extinction rate (rates for 40% reduction: 23 [fast] v. 21% [slow], $P = 0.86$; 35% reduction: 4 [fast] v. 7% [slow], $P = 0.54$). Having explored the behaviour of this rule, we now contrast its performance with that of alternative rules.

Does conspecific attraction provide an escape?

Conspecific attraction did not provide a generally effective escape (Fig. 2). All pairwise comparisons of the distributions of final population size were significant ($P_s < 0.006$), with the exception of the comparison between new (optimal) and philopatry (fast: $P = 0.90$, Fig. 2a; slow: $P = 0.96$, Fig. 2b). CA provided a partial escape in that it outperformed the completely naïve rule (i.e., where preferences were based on obsolete information reflecting conditions before the reduction in quality of habitat A). However, the performance by CA fell well short of that by both new and philopatric preferences.

Pairwise comparisons of extinction rates were significant (all nominal $P_s < 0.029$), with the exceptions of comparisons between new and philopatry for both life histories ($P_s = 1.0$) and comparisons between learning and both new and philopatry ($P_s = 0.059$) for fast life history. Thus, CA provided a limited escape as it led to a lower extinction rate than did the naïve rule (old) (fast: 6 v. 71%, $P = 6.8 \times 10^{-23}$; slow: 18 v. 55%, $P = 7.8 \times 10^{-8}$). But CA led to a higher extinction rate than did philopatry and new preferences (both 0%) (fast: $P_s = 0.029$ [nonsignificant following adjustment for multiplicity]; slow: $P_s = 3.3 \times 10^{-6}$).

The performance of CA was inconsistent relative to the learning rule. CA provided a more effective escape than learning for the fast life history (Fig. 2a; K-S test: $P = 6.9 \times 10^{-18}$; Fisher's exact test: 6 v. 48% extinction, $P = 8.2 \times 10^{-12}$) but a less effective escape for the slow life history (Fig. 2b; K-S test: $P = 0.006$; Fisher's exact test: 18 v. 5%, $P = 0.007$). This inconsistency reflects the fact that the learning rule performed much better for the slower life history (extinction rates: 5 v. 48%, $P = 1.4 \times 10^{-12}$). For the fast life history, individuals may not live long enough to provide an effective escape. But it also reflects the fact that CA was more successful for the faster life history (extinction rates: 6 v. 18%, $P = 0.015$). For the slow life history, individuals may live too long and so attract too many conspecifics to the now less suitable habitat to provide an effective escape.

The performance of CA also differed between fast and slow life histories depending on whether catastrophes occurred. When they occurred (with 3% probability per year), CA provided a better escape for the faster life history for both levels of habitat-quality reduction. In the absence of catastrophes, the reverse was true (results not shown). Generally, CA was more advantageous for the fast life history.

Philopatry mimicked the ideal despotic distribution, providing a complete escape (i.e. none of the populations went extinct); learning provided a more effective escape for the slower life history; and unchanged habitat preferences often led to extinction. Our novel finding is that CA provided only a partial escape, with some populations going extinct.

GENERAL DISCUSSION

Conspecific attraction (CA) did not provide an effective escape from the ecological trap (Fig. 2). Whereas the tendency to prefer the natal habitat (philopatry) provided a completely effective

escape (i.e. no extinctions), the tendency to settle near larger numbers of conspecifics (CA) sometimes led to extinction. Compared with philopatry, the bandwagon effect tended to jeopardize populations caught in the ecological trap. Individuals concentrated into the degraded habitat, and the aggregation of settlers in this sink habitat amplified its attractiveness to new settlers. CA did provide a partial escape in that it outperformed the worst-case scenario, where individuals were completely naïve to the habitat degradation and so preferred the sink habitat. But CA more typically led to “uncorrected” habitat preferences, shrunken populations, and heightened extinction risk.

Among the characteristics of organisms vulnerable to ecological traps are small population size, lack of flexible adjustment to environmental change, and reliance on indirect cues (Battin, 2004). To this list we add reliance on indirect *social* cues. Whereas using conspecific cues can dampen Allee effects in suitable habitats (Donahue, 2006), it can amplify them in ecological traps. Ordinarily, early-arriving individuals may fill up source habitats, forcing late-arriving individuals to spill over into sink habitats (Pulliam, 1988). But when source habitat is cryptically converted into sink habitat, an ecological trap is set and animals will tend to concentrate in the now-attractive sink, which can drastically suppress population growth (Kristan, 2003) and lead to extinction even when sink habitat comprises a small fraction of the total (Donovan & Thompson, 2001). Even small increases in availability of attractive sinks can have major effects (Delibes, 2001). But this false attractiveness may be especially problematic for species using CA, where early settlers serve as lures for subsequent settlers. This behaviour-mediated Allee effect could dramatically elevate extinction risk. CA may prove to be an important contributor to extinction proneness, perhaps especially for avian populations facing environmental change (Reed, 1999).

More optimistically, conspecific attraction did outperform the learning rule under the fast life history (Fig. 1a). Due to poor survival and high reproductive output for this life history, most individuals in each generation were yearlings selecting a habitat for the first time. In nature, these naïve settlers lack breeding experience and so are expected to capitalize on conspecific cues (e.g. Muller *et al.*, 1997). Attraction to conspecifics can spare settlers the cost of breeding failure elsewhere. But in our study, while CA provided a better escape than learning, it did not provide a generally effective escape because early-arriving conspecifics were explicitly not honest indicators of habitat quality (Doligez, 2003).

This insight has obvious conservation implications. Managers using conspecific cues to establish breeding populations in unoccupied habitats (e.g. Kress, 1983; Kress & Nettleship, 1988; Podolsky, 1990) should avoid doing so in sink habitat. These artificial cues should be honest indicators of underlying habitat quality. They should reduce search costs and aggregate individuals in high-quality habitats (Fletcher, 2006). Otherwise, a seemingly successful effort could do more harm than good, especially if colonists serve as lures for subsequent settlers. For example, it would make no sense to use conspecific cues to attract black-capped vireos (*Vireo atricapilla*) to unoccupied habitats where brood parasitic brown-headed cowbirds (*Molothrus ater*) would then cause complete breeding failure (Ward & Schlossberg, 2004). We offer this caution because conspecific cues are so powerfully attractive (e.g. Jeffries & Brunton, 2001) and because seemingly suitable habitats can be sinks.

Conspecific cues may be reliable indicators of habitat quality under prevailing conditions, but when ecological traps are set, conspecific cueing can lead to extinction. Managers should recognize that ecological traps might be especially problematic for animals that use conspecific cues. Compared with philopatric species, those using conspecific cues may need more intensive

conservation planning. The disparity in the performance of CA versus philopatry prompts several suggestions for future work. First, we should characterize species as exhibiting CA versus philopatry (Danchin *et al.*, 1998). Second, we should test the hypothesis that species using CA are more extinction prone than philopatric species. Finally, we should explore more fully the conditions under which CA might rescue populations from ecological traps versus drive them towards extinction. As human activities continue to alter the natural world, it is important to recognize that animals that use conspecific cuing may be especially vulnerable.

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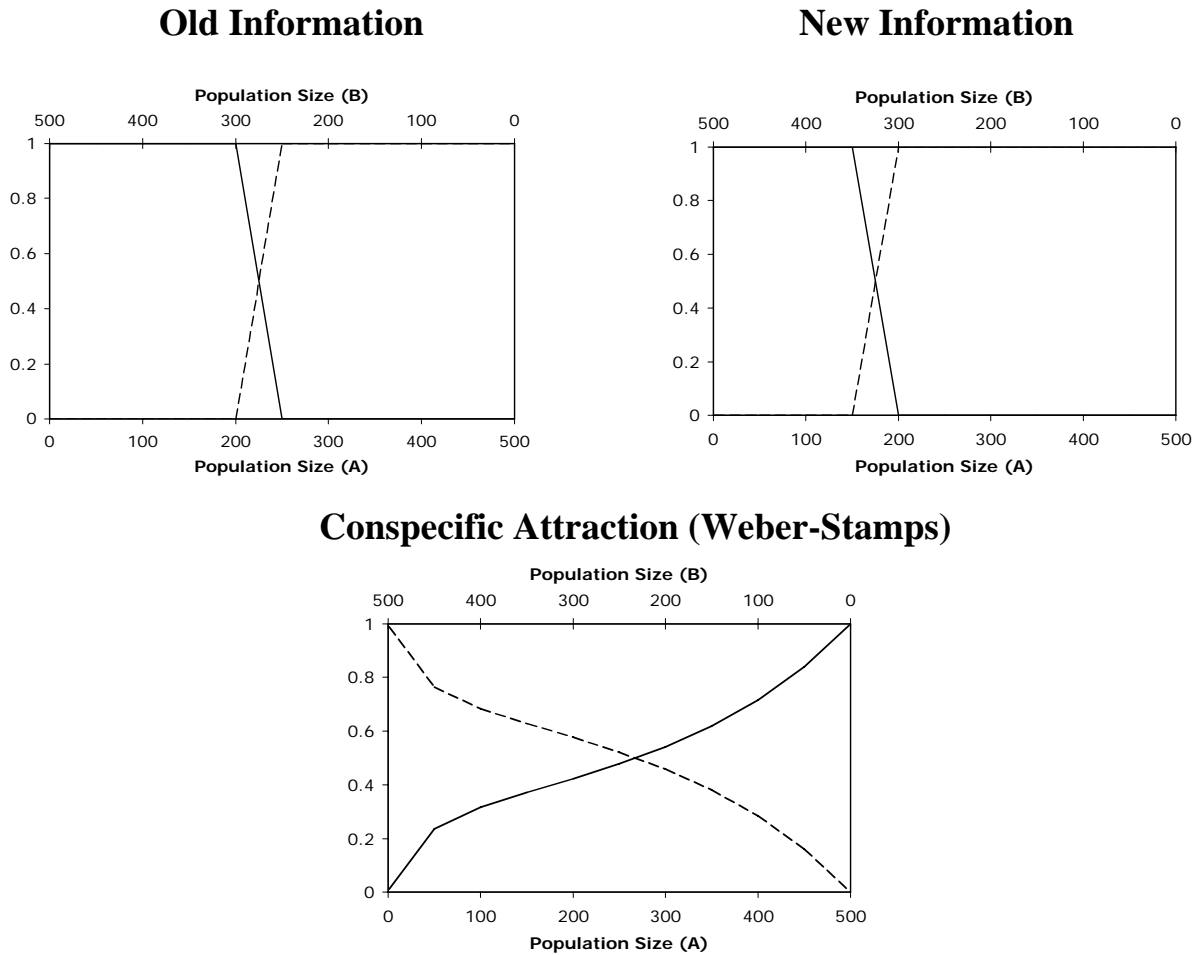


Figure 1. The probability of choosing Habitat A or B under various hypothetical combinations of population sizes. Solid line – probability of choosing Habitat A; Dashed line – probability of choosing Habitat B. When one habitat has many individuals relative to the other, conspecific attraction overwhelms the appeal of high-quality, unoccupied sites in the less populated habitat.

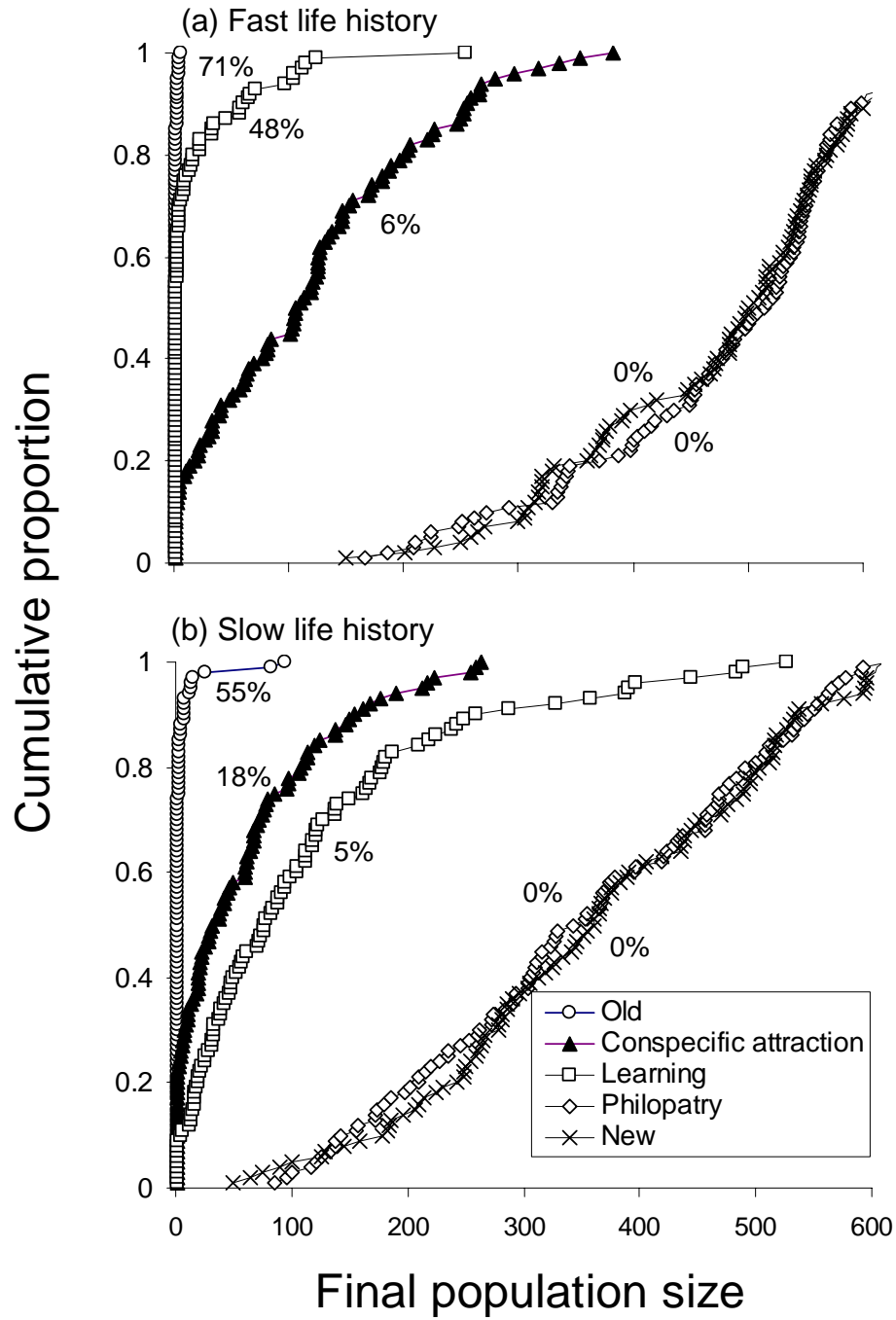


Figure 2. Cumulative frequency distribution of final population size (100 simulations run for 200 years), for several habitat-selection rules and two life histories. Observed percent of populations going extinct (following a 40% reduction in the quality of habitat A) under each habitat-selection rule is shown next to the trajectory. Parameter values: $C = 0.03$ and $\alpha = 0.6$ (both panels), $S = 0.8$ and $B = 1$ (panel a), $S = 0.5$ and $B = 4$ (panel b).